

## MECHANICAL PROPERTIES AND LOCOMOTOR FUNCTIONS OF EEL SKIN

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The functions of fish skin are numerous, and are generally categorized as forms of protection from or adjustment to the environment. Eel skin in particular performs these functions admirably. The fact that tanned eel skin has been used as door hinges in Scandinavia (Knut Schmidt-Nielsen, personal communication) attests to its toughness. With its ability to produce copious quantities of mucus the skin can also assist the animal in adjusting to rather extreme environmental conditions—eels are not only euryhaline but are also capable of aerial cutaneous respiration (Berg and Steen, 1965).

While performing these functions the skin must also provide both a rigid framework to support the body contents and a flexible covering to allow whatever changes in shape are necessary for locomotion. A system of collagen fibers in the skin of fishes arranged in alternating layers forming right and left helices about the long axis of the animal allows for shape changes. This highly ordered arrangement has been described for elasmobranchs (Motta, 1977; Wainwright, Vosburgh & Hebrank, 1978) and teleosts (Fujii, 1968; Nadol, Gibbons and Porter, 1969; Brown and Wellings, 1970; Hawkes, 1974; Smith, 1956; Willemse, 1972; Videler, 1975).

Engineers will recognize this design feature; they have for some time been reinforcing thin-walled pressurized cylinders by winding them with inextensible fibers. Such a design creates a lightweight cylinder wall which is strong against explosion and has the additional advantage of permitting extensions in any direction except those of the fibers themselves, *i.e.*, they resist torsion of the cylinder. In the directions of the circumference and long axis of the cylinder the greatest range of extension is permitted, these are the directions which bisect the angles between a pair of crossed-helices. The angle that these helices make with the long axis of the cylinder is called the fiber angle. For a range of fiber angles excluding those very near  $0^\circ$  and  $90^\circ$ , the cylinder can be bent without kinking or wrinkling.

The convex side of a bent cylinder is stretched in the longitudinal direction and compressed in the circumferential direction; on this side the fiber angle decreases. The reverse occurs on the opposite, or concave, side. In this way the cylinder, or a fish, can undergo a range of movements without changing its body form or volume (Clark, 1964), and without kinking or wrinkling.

With their study of shark skin, Wainwright *et al.* (1978) provide the first demonstration of the importance of a crossed-fibrillar array of collagen to fish locomotion. These authors found the skin acts as an external tendon, transmitting force and displacement in parallel with the attached, underlying muscles. Because a force applied to the skin generates a greater bending moment than the same force applied near the backbone, the mechanical advantage of the axial musculature is enhanced by skin capable of transmitting forces down the length of the fish.

Like the shark, the eel swims by undulatory propulsion, but differences in

body form between the two are apparent. The shark is constructed with the bulk of its musculature far anterior to its primary propulsive surface—the caudal fin. The eel has its musculature distributed more evenly along its length, and uses nearly this whole length as its propulsive surface—it lacks a distinct caudal fin. While it is easy to imagine the benefits an external tendon could provide the shark, *i.e.*, a mechanism for transmitting forces generated by the muscles to the tail, we might wonder whether similarly constructed skin could benefit the eel.

In view of the morphological differences between sharks and eels, the purpose of this study was to investigate the structural features and mechanical properties of eel skin as they relate to the locomotor behavior of the fish.

#### MATERIALS AND METHODS

*Experimental animals.* Eleven adult American eels (*Anguilla rostrata*) ranging in length from 41 to 64 cm were used for the mechanical tests and locomotion studies described below. They were obtained live from brackish intracoastal waters of North Carolina from Manteo to Wilmington, and kept in aquaria at native salinity until killed. Skin was removed from the refrigerated carcasses as needed. For histological studies, skin of the adult eels described above was used, as well as that of several elvers, the smallest of which was 20 cm in length. These were obtained by seining in fresh water creeks in North Carolina, and were kept frozen until studied.

*Structure of the skin.* Cryostat (American Optical, Model 830) sections ten microns thick were made from fresh skin samples, mounted on slides with distilled water, and examined using a Leitz Ortholux polarized light microscope equipped with a first-order red compensator. Other samples were fixed in 10% formalin, sectioned and stained with Verhoeff's elastin stain according to the procedure outlined in Humason (1962). Fresh skin samples were examined using a Wild M-5 dissecting microscope in order to determine the fiber angles. This was accomplished using the protractor stage of the microscope.

*Mechanical testing.* To test for elasticity in eel skin, several types of stress-strain tests were conducted. Uniaxial tensile stressing tests were performed on skin samples in order to quantify stress-strain relationships in the direction of the collagen fibers and in both the longitudinal and hoop (circumferential) directions. Square or rectangular skin samples measuring several centimeters on a side were cut from the fish between the dorsal and anal fins, or in regions anterior to these, between the mid-dorsal and mid-ventral lines. As much muscle as was possible was removed from the skin using razor blades and scissors. Snap-swivels or alligator clips connected to eighteen-pound test fishing leader wire were attached to the edges of the samples for testing in a stress-strain machine described elsewhere (Wainwright *et al.*, 1978). To test for extension in the actual fibers within the skin, samples were cut and stressed at 45° to the long axis of the animal (the fiber angle determined in prior dissections); during stressing the orthogonal sides of the skin were allowed to deform freely. In a similar manner skin was cut and stressed uniaxially in the hoop and longitudinal directions.

An additional series of stress-strain tests was conducted by applying an increasing tensile load to the longitudinal axis while maintaining the hoop axis at a constant stress. In order to maintain this constant stress the hoop sides were

allowed to compress or extend as necessary during the extension and compression of the longitudinal sides. The primary purpose of these biaxial stressing tests was to determine the relative contributions of the crossed-fiber system and the interfibrillar matrix material to the mechanical properties of the whole skin. If the extensibility of the skin is controlled solely by the helical fibers, the ratio of the hoop to longitudinal stresses applied is always equal to the tangent of the fiber angle resulting from these stresses times the tangent of the initial fiber angle. Using this relationship a longitudinal stress-strain curve can be constructed for any constant hoop stress applied, that will predict skin properties if they are due only to a set of continuous fibers. Comparison with the experimentally obtained stress-strain curve for whole skin should allow the role of the interfibrillar matrix to be assessed.

The secondary purpose of this experiment was to test for isotropy in the hoop and longitudinal directions predicted by a  $45^\circ$  fiber angle. To do so the experimental conditions were simply reversed and applied to previously untested samples, so that an increasing tensile stress was applied to the hoop axis while the longitudinal axis was maintained at a constant stress.

*Extensions of the skin during swimming.* Stress-strain curves for the skin cannot be very meaningful to our understanding of fish locomotion unless we know where the range of *in vivo* stresses and strains falls on the experimentally determined stress-strain curves. For this reason extensions of the skin in the hoop and longitudinal directions were measured in the following way: An eel was anaesthetized by covering it with ice for 2 to 3 hr, then 4 stitches were sewn in the skin on the side of the animal with heavy white thread. The four knots thus made formed a rectangle centered over the lateral line and an imaginary line running dorsoventrally located about three quarters down the eel's length. The eel was then warmed gradually and returned to an aquarium, after which it appeared to behave normally.

The following day the eel was placed in a circulating flow tank and filmed first from the side and then from above, using a Canon Scoopic 16-mm cine camera equipped with a close-up lens. The films obtained were analyzed using a

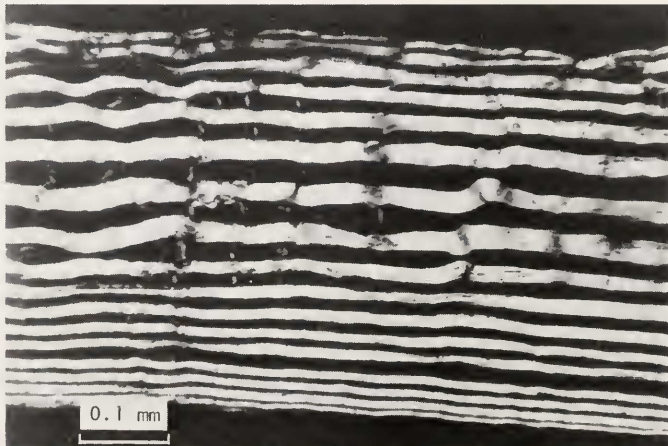


FIGURE 1. Polarized light micrograph of a radial section of eel skin cut parallel to one set of fibers. Seventeen fibers (or fiber layers) are seen in long section and six radial fibers are visible in the left half of the section.

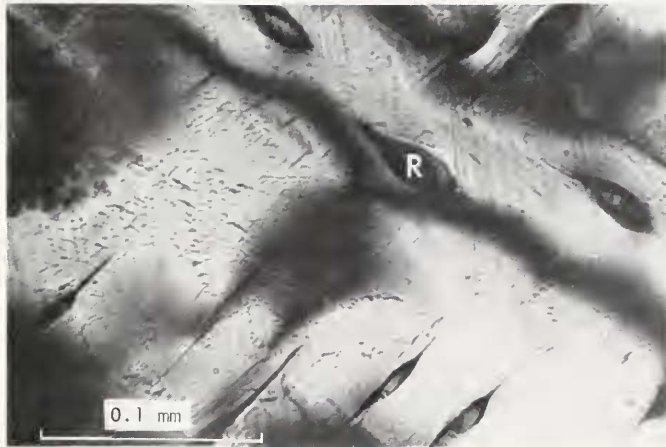


FIGURE 2. Polarized light micrograph of a tangential section of the fibrous region of eel skin. The long axis of the photograph is approximately parallel to the long axis of the fish. R, transverse section of radial fiber.

Perceptoscope; in the analysis the distances between the projected images of the pairs of knots were measured to the nearest  $1/50$  mm on the fish with vernier calipers.

## RESULTS

*Structure of the skin.* Eel skin differs from the skin of most teleosts in that the cycloid scales are completely embedded in the skin and are more or less isolated from each other (van Oosten, 1957). The pattern of the scale arrangement, however, can be readily observed without dissection due to the pigmentation in the outer layer of the skin which demarks the underlying scales. The oblong scales generally lie with their long axes oriented at an angle of about  $45^\circ$  to the long axis of the animal, but very close to the mid-dorsal line the scale angle decreases to as little as about  $10^\circ$ . The scales can be seen to lean both dorso-cranial and dorsocaudal, and these two orientations appear to be distributed randomly, giving the skin a shingled appearance. Surrounding the scales is a gelatinous material, under which lies a thick layer of collagen fibers. Microscopy reveals that alternating sheets of parallel fibers comprise this layer. Figure 1 is a polarized light micrograph of a section cut perpendicular to the skin and parallel to one set of fibers; seventeen fibers (one per layer) can be seen in long section. At the upper and lower boundaries of the dense fibrous layer the fibers are smaller in diameter. Interspersed through the helically-wrapped fibers are radially oriented fibers. These are seen in cross-section in the photomicrograph shown in Figure 2. The diameter of the radial fibers is approximately equal to that of the helical fibers; they are generally round in cross-section but may become distorted where they intersect the helical fiber layers. Beneath the fibrous layer is the subcutis, onto which the underlying muscles insert obliquely.

Fixed sections of eel skin stained negatively with Verhoeff's elastin stain. Counterstaining in Picro-Ponceau indicated that both the helical and radial fibers are probably composed of collagen.

The skin thickness and fiber diameter were found to increase with increasing



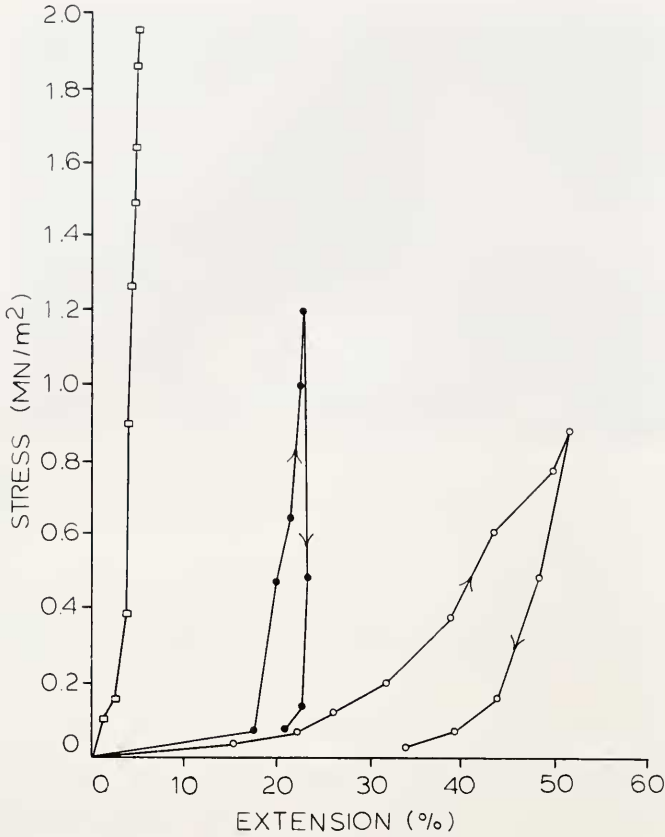


FIGURE 3. Typical stress-strain curves for eel skin stressed uniaxially in three directions. Open box, skin stressed in the direction of one set of fibers; closed circle, skin stressed in the hoop direction; open circle, skin stressed in the longitudinal direction. Loading and unloading curves are indicated by arrows for skin stressed in the hoop and longitudinal directions.

body length. A 20-cm long elver had skin 150 to 180- $\mu\text{m}$  thick and fibers of diameter ranging from about 5 to 10  $\mu\text{m}$ , while a 56-cm adult had skin 500 to 530- $\mu\text{m}$  thick and fibers of about 10 to 25  $\mu\text{m}$  in diameter. The elver's skin contained 11 to 13 pairs of fiber sheets and the adult's had 14 to 16 pairs.

Microscopy reveals that the long axes of the scales indicate the angle of the underlying collagen fibers. This is not true near the mid-dorsal line, however, where the scale angle becomes very low but the fiber angle does not change as the mid-dorsal line is traversed. A fiber angle of about  $45^\circ$  was found to prevail throughout the length of the fish (mean fiber angle =  $45.7^\circ \pm 4.7$ ,  $n = 87$ ). This angle is the same for both the anterior and posterior leaning fibers, and does not change through the lateral line.

*Mechanical testing.* In Figure 3 the results of three uniaxial stretching tests are shown in the form of stress-strain curves for skin stretched in the direction of one set of fibers and in the hoop and longitudinal directions. In the direction of the fibers very low extensions are obtained at high stresses. The fibers therefore appear to be reasonably inextensible, especially within the range of stresses applied

TABLE I

*Comparison of mean terminal elastic moduli (E) for eel skin stressed uniaxially in three directions*

Direction	
On-fiber	$E = 1.56 \times 10^8 \text{N/m}^2$ ( $n = 10$ , $s.d. = 1.44 \times 10^8$ )
Hoop	$E = 1.47 \times 10^7 \text{N/m}^2$ ( $n = 10$ , $s.d. = 1.28 \times 10^7$ )
Longitudinal	$E = 3.54 \times 10^6 \text{N/m}^2$ ( $n = 10$ , $s.d. = 2.52 \times 10^6$ )

to the hoop and longitudinal directions. The elastic modulus obtained as an average of ten on-fiber pulls was  $0.16 \text{ GN/m}^2$  (gigaNewtons per square meter), which is slightly lower than the elastic modulus of  $0.43 \text{ GN/m}^2$  obtained by Hebrank and Vosburgh (in prep.) for shark skin fibers. An on-fiber unloading curve is not shown in Figure 3 because in general the loading and unloading curves for skin stressed in the direction of the fibers were so close to one another as to be within the limits of resolution of the measuring devices. I do not believe that viscous effects within the fibers make a significant contribution to short-term mechanical behavior.

The stress-strain curves for skin subjected to uniaxial stretching in the hoop and longitudinal directions reveal anisotropy in the mechanical properties of the skin. In both cases the skin deforms by a relatively large amount while the stress remains low, then following this the stress-strain curve becomes steeper as the skin no longer deforms as freely under the applied load. Skin stressed in the longitudinal direction undergoes much greater extensions before it becomes stiff compared to skin stressed in the hoop direction. When the curves become steep, the slope of the curve for skin stressed longitudinally is much less than that for skin stressed in the hoop direction. This difference in slope is equivalent to the difference in elastic moduli, or stiffness, of the skin when stressed in the two directions. The mean terminal elastic modulus (the elastic modulus in the steep part of the stress-strain curve) for skin pulled in the longitudinal direction is  $3.5 \text{ MN/m}^2$ , which is significantly lower ( $F_{(1, 18)} = 5.69$ ,  $0.025 < P < 0.05$ ) than that of skin pulled in the hoop direction, a value of  $14.6 \text{ MN/m}^2$ . Values for the mean terminal elastic moduli obtained by stressing skin uniaxially in the on-fiber, hoop and longitudinal directions are compared in Table I.

Breaking stresses and strains for skin pulled in any direction could not be determined. On application of high loads (on the order of  $2 \text{ MN/m}^2$  for hoop and longitudinally stressed skin, and  $3 \text{ MN/m}^2$  for skin stressed in the fiber direction) the skin always failed at the clips attaching the skin to the testing machine.

In general, skin samples did not return to their original lengths once the load was removed, indicating that some viscous flow within the skin occurred. The hysteresis in the loading and unloading curves further attest to this conclusion. The loss of strain energy is considerably greater for skin stressed in the longitudinal direction.

Stress-strain curves for tests in which one side of the skin was held at a constant stress while the orthogonal side was subjected to an increasing tensile load begin to clarify the nature of the anisotropy noted above. A stress-strain curve for a test performed in which the hoop axis was maintained at a stress of

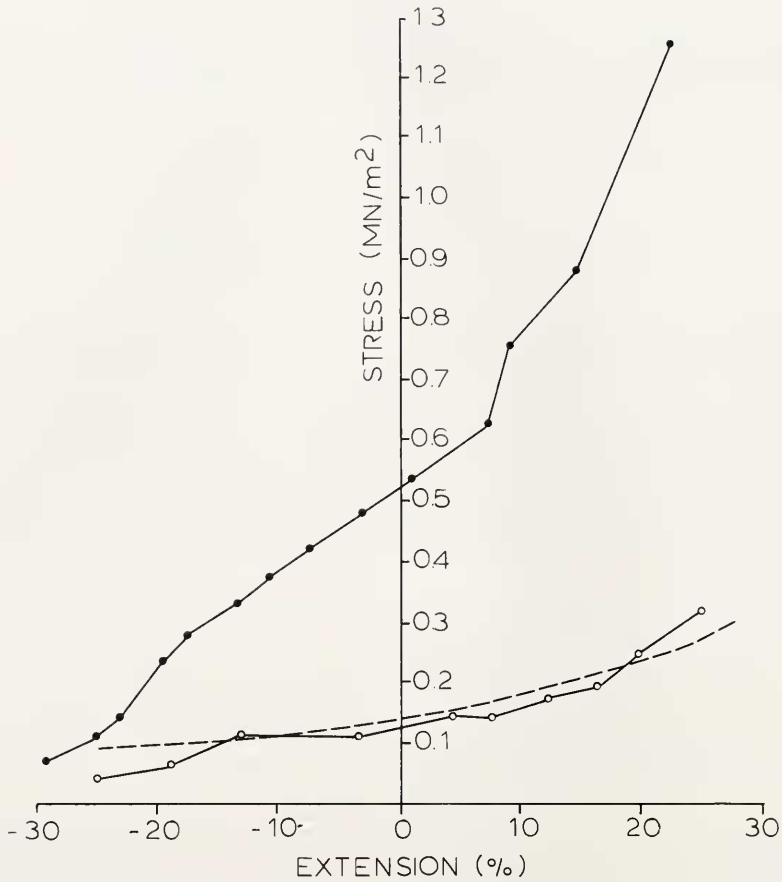


FIGURE 4. Stress-strain curves for tests in which one side of the skin was held at a constant stress while the orthogonal side was subjected to an increasing tensile load. Closed circle, hoop direction pulled while longitudinal direction held at stress of  $0.16 \text{ MN/m}^2$ ; open circle, longitudinal direction pulled while hoop direction held at stress of  $0.15 \text{ MN/m}^2$ . A theoretical curve for a pure fiber model subjected to the same ratio of forces is shown as a dashed line.

$0.15 \text{ MN/m}^2$  is shown in Figure 4. Also in this figure is a graph of a calculated curve, based on the continuous fiber model described previously, subjected to the same ratio of forces applied to the skin. It can be seen from these graphs that the crossed-fibers within the skin behave in a manner similar to the model except at the end points of the curves. In the range of  $\pm 10\%$  extension, the elastic modulus of the eel skin was found to average  $0.39 \text{ MN/m}^2$ , while that of the model shown averages about  $0.35 \text{ MN/m}^2$ , an insignificant difference. The departure of the experimental curve from the model curve at the end points indicates that the matrix material, the interference between the helical and radial fibers, or some other feature of the skin may become a limiting factor at very high and low fiber angles, or that the density of fibers or their thickness may similarly impose limits to extension.

When the experimental conditions were reversed and the longitudinal axis was maintained at a stress of  $0.16 \text{ MN/m}^2$ , the stress-strain curve for the hoop

direction shown in Figure 4 was obtained. By comparing this curve to that shown for skin stressed in the longitudinal direction and to the theoretical curve, it is readily apparent that skin stressed in the hoop direction does not behave like a pure crossed-fiber system. In the  $\pm 10\%$  extension range, the elastic modulus of  $13.7 \text{ MN/m}^2$  for hoop extension is two orders of magnitude higher than those obtained for longitudinal extension and the pure fiber model.

*Extensions of the skin during swimming.* Of eighteen measurements of skin extensions in the circumferential direction, the maximum value obtained was  $\pm 11.4\%$  extension. However, in the film analysis it was impossible to tell when the body was exactly straight in the region of the skin markers, so this maximum may be an overestimation of *in vivo* extensions. Most of the measurements fell within the range of  $\pm 6-8\%$  extension, so it is felt that this is a reasonable approximation of circumferential skin extensions during swimming. The maximum longitudinal extension measured was  $\pm 25.3\%$  ( $n = 23$ ), however longitudinal extensions generally fell between  $\pm 10$  to  $15\%$ . Since the curvature of the eel's body could not be fully incorporated into the measurements, this range of longitudinal extensions may underestimate actual skin extensions by several percent. It should be emphasized that these measurements are meant only to establish an approximate range of *in vivo* extensions of the skin during swimming.

## DISCUSSION

The large proportion of collagen fibers within the skin of *Anguilla rostrata* accounts for the skin's strong construction. In consideration of the skin's mechanical properties relevant to locomotor movements, the effects of the radial fibers were assumed to be negligible, and thus only the helical fibers were tested mechanically.

Uniaxial stressing tests illustrate several important properties of crossed-fiber systems. Skin stressed in the direction of the fibers is quite stiff, indicating that the fibers within a skin sample are effectively continuous. The continuity of the fibers is also indicated by the histological evidence; disruptions in the fibers were never observed. Skin stressed in either the hoop or longitudinal directions shows characteristic J-shaped stress-strain curves. Here the skin elongates considerably at low stresses, and this horizontal part of the stress-strain curve corresponds to rearrangement of the two sets of fibers relative to each other, *i.e.*, a change in fiber angle. The steep part of the curve corresponds to more direct loading of the fibers, for at this point the fiber angle has changed so as to nearly align the fibers with the applied load. Now the material deforms less readily under the load, and the elastic modulus increases accordingly.

While skin stressed uniaxially in the hoop and longitudinal directions shows similar qualitative behavior, we have already noted the differences in quantitative behavior, with skin stressed in the hoop direction being stiffer by an order of magnitude than skin stressed in the longitudinal direction.

This anisotropy is more pronounced in the biaxial stressing tests, in which one direction of the skin was held at a constant stress while the stress applied to the orthogonal direction was varied. We have already noted that skin stressed in the longitudinal direction behaves like a pure fiber system, at least within the range of *in vivo* extensions of the skin. Skin stressed in the hoop direction, however, behaves like a composite material of higher elastic modulus than that of the pure fiber model. Clearly something is limiting hoop extension in eel skin.



It is surprising that skin composed of crossed fibers oriented at  $45^\circ$  should be anisotropic in the hoop and longitudinal directions. Here, barring asymmetrical interference from the matrix material surrounding the fibers, the skin should be capable of extending as freely in one direction as in the orthogonal direction. Skin made up of fibers oriented at angles other than  $45^\circ$  would be expected to show anisotropic properties, since the degree of extension is a function of the initial fiber angle (Clark and Cowey, 1958). For example, crossed-fiber helices forming angles higher than  $45^\circ$  with the long axis of the body would resist hoop extensions while permitting longitudinal extensions, and should therefore exhibit a higher elastic modulus in the hoop direction. The fact that eel skin behaves like skin having a fiber angle greater than  $45^\circ$  suggests that other components of the skin make important contributions to its mechanical properties.

If the eel can be thought of as a pressurized cylinder (a reasonable assumption, since muscular contraction most likely creates at least transient pressurization within a myomere), an additional feature within the skin which acts to limit hoop extension would be of benefit to the animal. For a thin-walled cylinder wrapped with helical fibers and pressurized within, the hoop and longitudinal stresses in the walls of the cylinder are balanced when the fiber angle is  $55^\circ$  (Wainwright, Biggs, Currey and Gosline, 1976). This means the pressure within the cylinder may be accommodated without changing the shape of the cylinder; aneurisms will never develop. If the fiber angle is less than  $55^\circ$ , some additional mechanism is required to take up circumferential stresses within the cylinder wall, and it appears that eel skin may have that mechanism.

Mittal and Bannerjee (1974), using Verhoeff's staining method, report the presence of elastin fibers intermingled with fine collagen fibers in the dermis of the freshwater teleost *Notopterus notopterus*, however, they give no clue as to the orientation of these fibers. Elastin fibers, if oriented in the direction of the circumference of the eel, might account for the mechanical anisotropy noted, but no elastin fibers were found in this study. It is believed that the protein matrix surrounding the collagen fibers will be found to be responsible for the anisotropy of eel skin, and chemical and mechanical tests are currently being undertaken to determine the nature of the matrix material.

Fujii (1968, p. 102) viewed the primary function of the collagenous layer of fish skin as a means "to strengthen the thin integument of the animal to protect it from splitting under tensile force." From the stressing tests described here we can see that eel skin is strong in tension. Videler (1975, p. 192), in his studies of the cichlid *Tilapia nilotica*, suggested that the skin is too strongly constructed to simply "pliantly conform to the muscle waves." Videler believes that during bending of the fish, the fiber angle does not change, and so forces of equal magnitude must be applied to the skin in the hoop and longitudinal directions. He concludes that tension in the skin must remain constant during a swimming stroke in order for transmission of force from the axial musculature to the tail to be accomplished.

However, both Hebrank (this study) and Wainwright *et al.* (1978) found fiber angles to change during bending. It is these changes in fiber angle that allow the transmission of force through the skin during swimming. In a fish wound with helical fibers, muscle contraction in the anterior region bends the fish, and so the skin on the convex side is extended in the longitudinal direction. This extension, however, produces contraction in the hoop direction as the fiber angle decreases, until these dimensional changes are resisted by the pressurization of the body fluids beneath the skin. Now the skin becomes stiff, and further

longitudinal force applied to the skin by the anterior muscles results in tension transmitted to the tail through the skin. In this way the skin of fishes can act as an external tendon, as suggested for sharks by Wainwright *et al.* (1978).

It might appear, however, that an external tendon of this nature would be of less benefit to an eel than it would be to a shark. It should be kept in mind though, that both the eel and the shark swim by undulatory propulsion, and in both cases the amplitude of the waves of bending increases as these waves travel backwards (Gray, 1933), while the mass of the musculature decreases down the length of the body. Thus, in spite of the differences in distribution of the propulsive surfaces, the skin of both fishes may serve a similar locomotor function.

In addition, the eel exhibits another type of locomotor behavior in certain feeding situations. When the eel feeds on something which is too large to swallow, it bites into the food and then rotates about its own long axis several times, with great speed, in order to tear off the mouthful (Tesch, 1977; Moriarty, 1978). This motion can sometimes be seen when an eel is caught on a hook and line, and it has been witnessed in eels in aquaria.

When this "corkscrew" motion occurs, the eel's skin must be stressed in torsion. A cylinder wrapped with inextensible fibers resists torsion most rigidly when the fibers are wound at an angle of  $45^\circ$  with the long axis (the direction of maximum tensile stress during torsion). Thus, when the eel performs its corkscrew motion, the collagen fibers of one helical set (either the right- or left-helical set, depending on the direction of the motion) are being pulled along their long axes. Since the fibers behave as though they are continuous, the tensile force is transmitted along the length of the fish. In this way it is possible that the eel need only generate a twisting moment about the head in order to rotate the whole body. It appears that a fiber angle of  $45^\circ$  is uniquely suited to this corkscrew motion.

Thanks are due to S. A. Wainwright for helpful discussions and advice throughout this study, to J. H. Hebrank for valuable technical assistance, and to C. A. Johnson and F. Hinshaw for supplying most of the animals used in this study. This work was supported in part by a Cocos Foundation Training Grant in Morphology.

#### SUMMARY

1. The skin of the American eel *Anguilla rostrata* is composed largely of a crossed-helical array of fibers, believed to be collagen, that are oriented at an angle of  $45^\circ$  with the long axis of the fish. Uniaxial and biaxial tension testing of eel skin was used to assess the role of the collagen fibers in the locomotor functions of the skin.

2. The elastic modulus of skin stressed in the circumferential direction of the fish is  $14.6 \text{ MN/m}^2$  while that of skin stressed in the longitudinal direction is  $3.5 \text{ MN/m}^2$ , thus eel skin is an order of magnitude stiffer in the circumferential than in the longitudinal direction. The skin is stiffest in the direction of the fibers, having an elastic modulus of  $0.16 \text{ GN/m}^2$  in this direction. Within the range of *in vivo* extensions the behavior of skin stressed in the longitudinal direction is similar to that of a model consisting of continuous crossed-fibers, while that of skin stressed in the circumferential direction is not.

3. The mechanical behavior of the skin indicates that the skin may act as an external tendon, transmitting forces arising in the axial musculature down the length of the fish to the tail.

4. The collagen fibers within the skin may play an important role in torsion resistance when the eel executes its peculiar "corkscrew" motion.

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